BIOSONAR PERFORMANCE AND PROCESSING IN FM BATS

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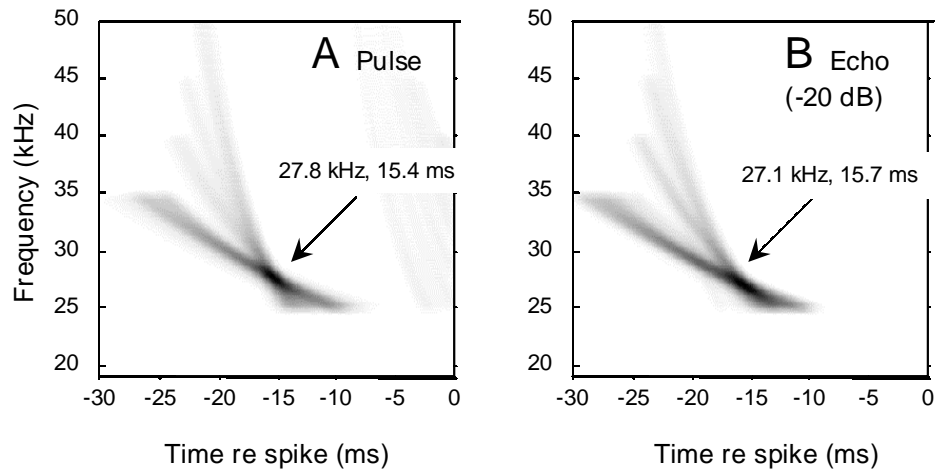Prescribed by ANSI Std Z39-18

Fig. 6. Identification of the excitatory FM-sweep frequency for a representative IC neuron by reverse correlation (REVCOR) analysis, a method that searches over the time-interval prior to each spike to find any common element in all the stimuli that precedes responses. Graphs show the frequency which drives responses to simulated sonar *pulses* (**A**) or *echoes* (**B**) for fixed FM sweep-widths with different durations and thus different sweep rates. In each plot, the shaded FM sweeps with different slopes appear to rotate about a common point in time-frequency space at about 27-28 kHz and a fixed time of about 15-16 ms prior to the neuron's spikes. This is a unique point because the response is just one spike per sound. The point identifies the location along the sweep that delivers excitation to the cell and registers the cell's characteristic latency (its "delay-tap" value). This point also specifies the time and frequency dimensions of a new time-frequency representation that the IC substitutes for the original spectrogram created by the inner ear.
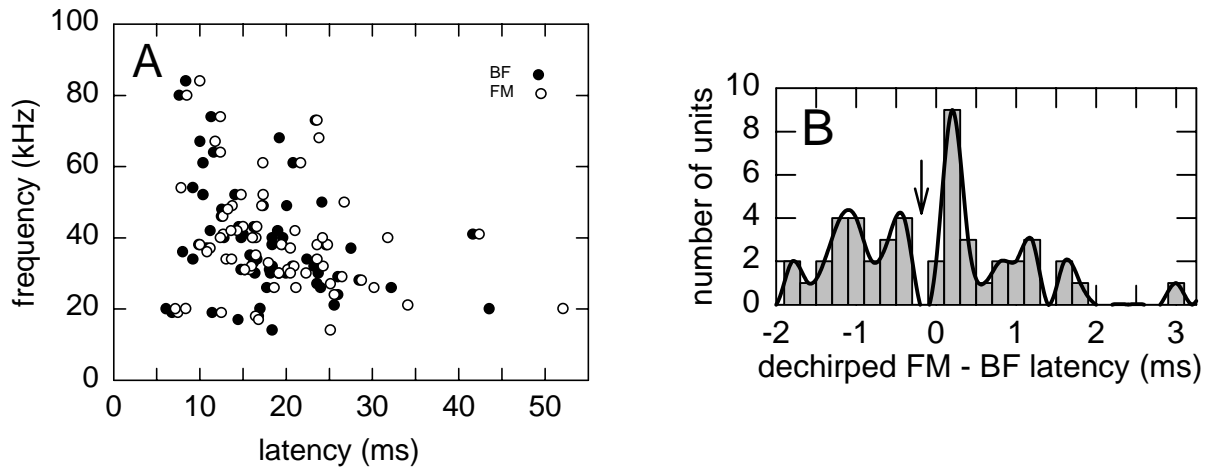

Fig. 7. (**A**) Neurons in the bat's inferior colliculus are tuned to a specific best frequency (BF) from 10 to 100 kHz and have a characteristic latency at BF (filled circles). They respond to FM sweeps by registering the time of BF in the sweep (instantaneous frequency) with a single spike at that characteristic latency (open circles). (**B**) When latency is compensated for time-of-BF in the sweep (sweep is "dechirped"), the spike latency is either aligned just after the time of BF (major histogram peak) or in a periodic pattern around the time of BF. The narrow region of no responses immediately prior to BF (arrow) reflects the presence of inhibition that is responsible for creating the relatively long response latencies.
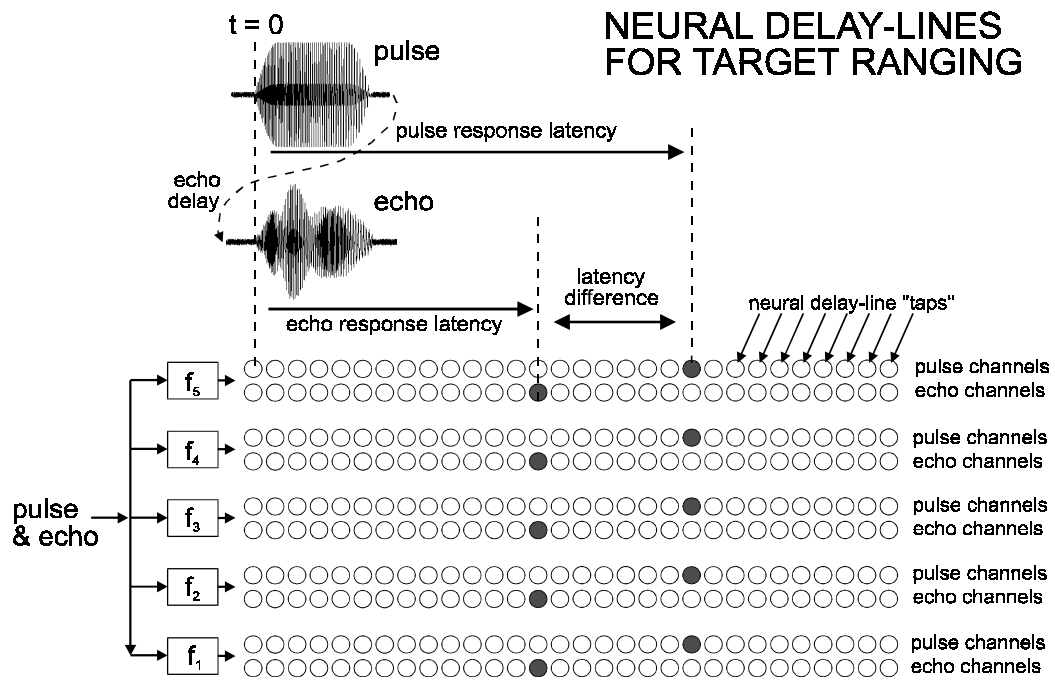
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Fig. 8. Diagram showing hypothetical physiological delay-lines for determining target range from echo delay. The delay-line/coincidence-detector model extracts echo delay from the latencies of neural responses to the pulse and the echo, which travel along separate delay-lines. Individual delay-line "taps" correspond to responses of neurons in the IC tuned to different frequencies and having different characteristic latencies (see Fig. 8A). If the delay of the echo is equal to the latency difference between the pulse and the echo responses, these responses will occur simultaneously in both cells and will trigger a response in a coincidence-detecting neuron at the next stage in the processing sequence. Coincidence-detector neurons are found in the auditory midbrain and cortex (see Fig.) and are tuned to delays corresponding to the entire 5-m operating range of the big brown bat's sonar.

Fig. 9. *Due to a state of adaptation normally prevailing during active echolocation, inferior colliculus responses to sonar pulses and echoes consist of just one spike to either sound, not multiple spikes.* The graph shows the number of spikes per broadcast sound or per echo evoked by broadcasts and echoes presented in the natural pattern of durations, repetition-rates, and echo delays during pursuit of flying insects. Because each sound evokes at most a single spike in any given neuron, processing of information in echoes must consist largely of neural computations carried out on the latencies of responses. If each neuron spikes only once, the time-of-occurrence of that spike is the only useful information it conveys. This means that a realistic computational model of echolocation has to be capable of producing full-scale sonar images using only numerical manipulations of latencies distributed across large numbers of frequency-tuned channels.
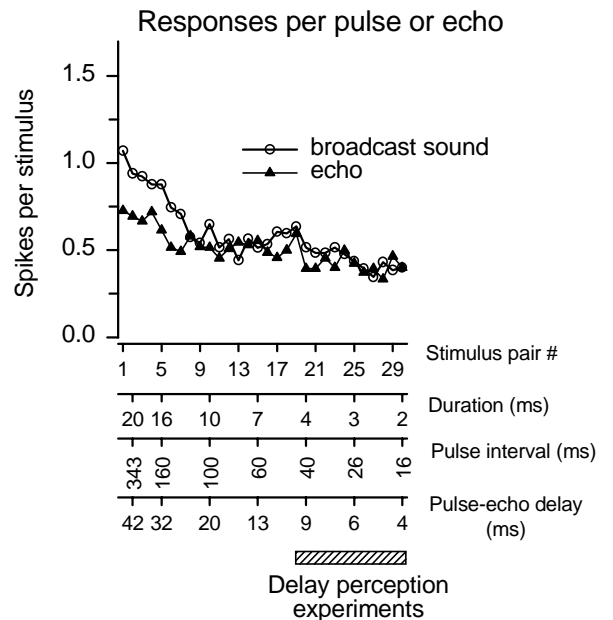

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Fig. 10. Histogram showing distribution of best delays for delay-tuned neurons in the big brown bat's auditory cortex. The bat processes delays from at least 1-2 ms to about 30 ms and beyond. These delays correspond to target ranges from 30 cm to about 5 m. Compare this distribution with the distribution of delay-line taps represented by the latencies in Fig. 7A.
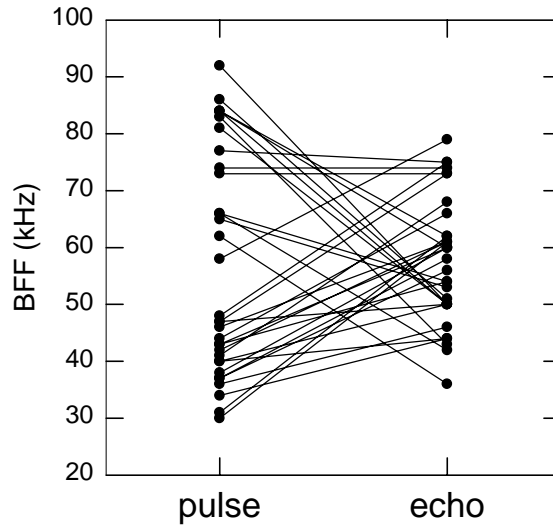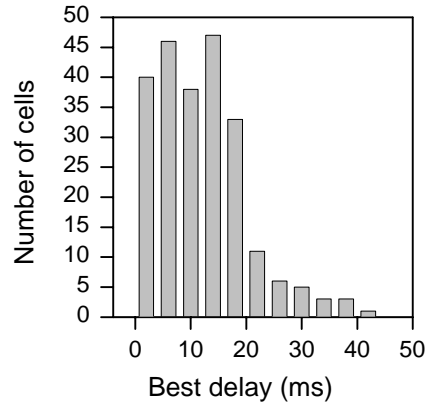

Fig. 11. Graph showing relation between the best facilitation frequency (BFF) selected from the broadcast sound (pulse) and the BFF from the echo for delay-tuned neurons in the big brown bat's midbrain. These cross-frequency comparisons implement a broader class of latency-measuring algorithms than just spectrogram correlation. Coincidence detectors for reading out delay-line time values only register true echo delays if all pulse and echo comparisons make place at the *same* frequencies. The neural coincidence detectors actually found in bats make pulse-echo comparisons across *different* frequencies (BFFs), which places the time-of-occurrence of spectral features (peaks, notches) in the same domain of latency as echo delay, but on an expanded time scale. Cross-frequency coincidence detectors may execute the deconvolution required to bring target shape back into spatial dimensions from the frequency axis of time-frequency representations.